

A reconsideration of *Ellipanthus* (*Connaraceae*) in Madagascar and continental Africa, and a comparison with the species in Asia

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Summary : As a result of the discovery of some mislaid collections of *Ellipanthus* from Madagascar (which were overlooked up to now) a new study has been made of *Ellipanthus* in Africa, and a comparison has been made with *Ellipanthus* in Asia. *Ellipanthus madagascariensis* (Schellenb.) Capuron ex Keraudren is evidently conspecific with *E. hemandradenioides* Brenan from eastern mainland Africa. An attempt is made to reconstruct the phylogeny of the entire genus, and the pattern of geographical distribution is discussed.

Résumé : Des spécimens d'*Ellipanthus* de Madagascar ayant été récemment retrouvés, une nouvelle étude des espèces africaines de ce genre et une comparaison avec les espèces d'Asie ont été réalisées. *Ellipanthus madagascariensis* (Schellenb.) Capuron ex Keraudren est incontestablement conspécifique de *E. hemandradenioides* Brenan d'Afrique continentale de l'Est. Une tentative de reconstruction de la phylogénie de ce genre, ainsi que sa répartition géographique, sont présentées et discutées.

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I. INTRODUCTION

In the revision of *Ellipanthus* (LEMMENS, 1989) in the monograph of *Connaraceae* of Africa, it was assumed that only once a plant of this genus had been collected in Madagascar : *Baron 5626* (K). KERAUDREN (1958) also cited this single collection in the treatment of *Connaraceae* for the Flora of Madagascar. However, additional *Ellipanthus* specimens were collected during the 20th Century in Madagascar. They were in the possession of Dr CAPURON, and after his demise they were delivered to Dr KERAUDREN in Paris. Neither CAPURON, nor KERAUDREN published anything in reference to this herbarium material, but CAPURON made notes on the sheets. According to these notes, he intended to distinguish some new species. After her decease the specimens were found in Dr KERAUDREN's office, and were recently inserted in the general herbarium. When the present author was engaged in annotating *Connaraceae* in September 1989 they consequently came to his attention for the first time.

The material of *Ellipanthus* from Madagascar concerns 18 collections, and in addition a duplicate of the type specimen of *E. madagascariensis* (Schellenb.) Capuron ex Keraudren. Obviously this provides a much better representation of the variation of *Ellipanthus* in Madagascar, and it was the immediate cause for a renewed study of the genus, the results of which are presented in this paper.

II. OBSERVATIONS

1. ELLIPANTHUS FROM MADAGASCAR

Ellipanthus specimens have been collected in northern Madagascar and in the eastern part of central Madagascar (see Fig. 1). Plants have been found in forests at up to 700 m altitude, and they were described as small trees up to 20 m tall with trunk diameters up to 40 cm. In a single case (*SF 26811*) the wood is cited as being used locally for construction purposes.

The specimens are rather variable, especially in the shape and size of the leaves, in the length of the inflorescences, and, to a lesser degree, in the size of the flowers. There seems to be some correlation between this variation and the geographical distribution. In the southern part of the area of distribution, which covers the eastern part of central Madagascar, plants tend to have small, coriaceous and ovate leaflets and comparatively large flowers (*Louvel 46, 200, 230, SF 26811, SF 28405, SF 256R133*). In the north, plants with large leaflets and small flowers form the majority (e.g. *Baron 5626, Perrier de la Bâthie 2098*). However, there are several intermediate specimens, and these were collected throughout the area of distribution (*9993 RN, SF 9240, SF 11435, SF 19067, SF 30030*).

Some specimens have unisexual flowers : *SF 11435, SF 15920* (staminate), and *9993 RN* (pistillate). The occurrence of distinctly unisexual specimens in the genus *Ellipanthus* is consequently not restricted to Asia, as was supported previously (LEMMENS, 1989, p. 67-68, 269).

The follicles of *Ellipanthus* are dehiscent along a ventral suture, as is the case in all *Connaraceae* species with dehiscent follicles. However, the follicles of the specimens *SF 24905* and *SF 27724* show a dorsal suture. It is most likely that this is an artifact, caused by drying. A single follicle of *SF 27724* lacking a seed and clearly already open before drying, does show a ventral suture.

2. COMPARISON OF ELLIPANTHUS FROM MADAGASCAR AND EASTERN CONTINENTAL AFRICA

Ellipanthus shows little variation in all characters in eastern continental Africa (Kenya, Tanzania). After the study of the new material from Madagascar it now can be included conveniently within the variation of *Ellipanthus* in Madagascar. For instance, *Dale 3876*, the type specimen of *E. hemandradenioides* Brenan, is rather similar to *SF 8741, SF 27724* and *SF 30030* from Madagascar; *Reitsma & de Wilde 143* from Kenya also resembles *SF 8741* and *SF 27724*; *Faden & Faden 74/292* from Kenya resembles *SF 30030*; *Beentje 2314*, also from Kenya, is almost similar to *9993 RN*.

3. COMPARISON OF ELLIPANTHUS FROM AFRICA AND ASIA

In Asia, *Ellipanthus* has a large area of distribution. It extends from Sri Lanka to southern China and western Malesia. At least 5 species are distinguished in this area :

- *E. unifoliolatus* (Thwaites) Thwaites from Sri Lanka, the type species;
- *E. calophyllus* Kurz from the Andaman Islands;

- *E. glabrifolius* Merr. from southern China (Hainan);
- *E. tomentosus* Kurz from western Malesia;
- *E. beccarii* Pierre from Borneo.

The differences between these species are extremely subtle, as has been pointed out before (LEMMENS, 1989, p. 269). In addition some subtle differences between African and Asiatic specimens of *Ellipanthus* have been observed :

a. *Thwaites 2443* (K), the type of *E. unifoliolatus* is close to some Madagascar specimens such as *SF 24905*, *SF 27724* and *SF 28405*, but it differs in its more distinct venation of the upper surface of the leaf, in its sepals being pubescent inside and its petals being glabrous except on their margin. In the African specimens the sepals are glabrous inside while the petals are pubescent inside.

b. *E. calophyllus* differs from *E. unifoliolatus* by having a longer petiole. However, the scanty and incomplete collections of this species available to me do not allow a sound comparison.

c. *E. glabrifolius* also has a comparatively long petiole.

d. *E. tomentosus* is a variable species divided by LEENHOUTS (1958) into 2 subspecies and 2 varieties. It often has densely pilose lower sides of the leaflets, and it differs in that respect from African specimens which have glabrous or sparsely pilose leaflets. The leaflets of *E. tomentosus* are often quite large, while the inflorescences usually are short and compact. In some cases, however, African specimens can hardly be distinguished from *E. tomentosus*.

e. *E. beccarii* usually has 4-merous flowers which are unisexual as a rule. As was mentioned, unisexual plants are also found on Madagascar, but 4-merous flowers do not occur there.

III. RECONSTRUCTION OF PHYLOGENY

I have made an attempt to reconstruct the phylogeny of *Ellipanthus* by using the computer programme PAUP, version 2.4.1. For the construction of a matrix only 7 usable characters were available (see Table 1). However, in some species both character-states of certain characters are simultaneously present : *E. tomentosus* may have long petioles as well as short ones, and sepals pubescent as well as glabrous inside, whereas *E. madagascariensis* may have bisexual as well as unisexual flowers. Such situations are valued in the matrix as 3. In case a species only rarely shows one of the character-states it is disregarded and only the other, commonly present character-state is noted in the matrix (1 or 2). It appears that *E. calophyllus* and *E. glabrifolius* cannot be separated by the characters used for the phylogenetic analysis, and they are consequently considered as a single operational taxonomic unit (otu).

Connarus griffonianus Baillon is used as the outgroup. The phylogenetic analysis of the genera of *Connaraceae* (LEMMENS, 1989, p. 112) showed that *Connarus* is ancestral to *Ellipanthus*, and consequently a *Connarus* species resembling *Ellipanthus* in the fruits is chosen as outgroup. One of the results of the phylogenetic analysis is reproduced in Fig. 1. The cladogram presented is the most parsimonious tree out of the 105 trees found and with a minimum of trichotomous branching. The number of steps is 11, the consistency index 0.909.

TABLE 1 : Matrix of *Ellipanthus* species.

	a	b	c	d	e	f	g	character
<i>Connarus griffonianus</i> (outgroup)	1	1	1	1	1	2	1	
<i>Ellipanthus beccarii</i>	2	2	2	2	2	2	1	
<i>Ellipanthus calophyllus</i> + <i>glabrifolius</i>	2	1	1	1	1	2	1	
<i>Ellipanthus madagascariensis</i>	2	2	1	3	1	2	1	
<i>Ellipanthus tomentosus</i>	1	3	2	1	1	3	1	
<i>Ellipanthus unifoliolatus</i>	2	2	1	2	1	1	2	
otu								

Characters :

- a = leaves usually pilose beneath (1), or glabrous (2);
- b = petiole usually long (1), short (2), or both character-states possible (3);
- c = inflorescences usually long and lax (1), or short and compact (2);
- d = flowers usually bisexual (1), unisexual (2), or both character-states possible (3);
- e = flowers usually 5-merous (1), or 4-merous (2);
- f = sepals pubescent inside (1), glabrous (2), or both character-states possible (3);
- g = petals pubescent inside (1), or glabrous (2).

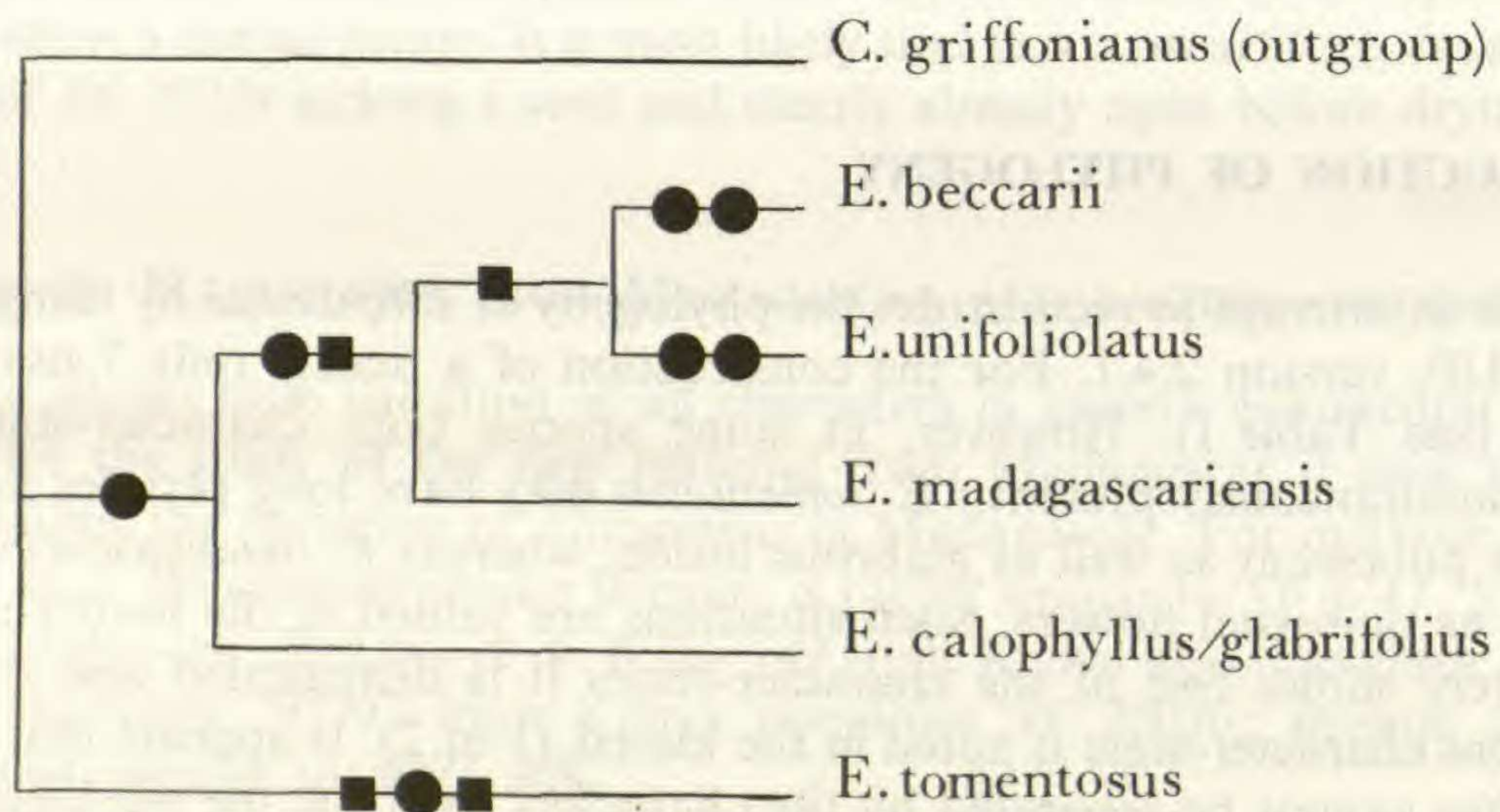


Fig. 1. — Cladogram of *Ellipanthus* species using *Connarus griffonianus* as outgroup.

IV. CONCLUSIONS AND DISCUSSION

1. TAXONOMY AND GEOGRAPHY

It has already been presumed that *E. madagascariensis* and *E. hemandradenioides* might be conspecific (LEMMENS, 1989, p. 274). The 'missing' material from Madagascar proves this supposition to be correct. As a result, only a single *Ellipanthus* species on the African continent, including Madagascar, is accepted :

***Ellipanthus madagascariensis* (Schellenb.) Capuron ex Keraudren**

Flore de Madagascar et des Comores, fam. 97 : 2 (1958); LEMMENS in BRETILER (Editor), The Connaraceae, a taxonomic study with emphasis on Africa : 272 (1989).

- *Hemandradenia madagascariensis* SCHELLENB. in ENGL., das Pflanzenreich 103 (4, 127) : 65 (1938). Type : Madagascar, probably NW, *Baron 5626* (holo-, K; iso-, P).
- *Ellipanthus hemandradenioides* BRENNAN, Hookers Icones Plantarum ser. 5, vol. 5 : tab. 3452 (1947); HEMSLEY, Flora of Tropical East Africa : 22 (1956); LEMMENS in BRETILER (Editor), The Connaraceae, a taxonomic study with emphasis on Africa : 269 (1989). Type : Kenya, Malindi Distr., *Mida, Dale 3876* (holo-, K; iso-, BR).
- *E. curvipetalus* CAPURON, *nomen in sched.*
- *E. dioicus* CAPURON, *nomen in sched.*

Shrub or small to medium-sized tree, up to 20 m tall with trunk diameter up to 40 cm. Branches terete, usually lenticellate, branchlets often somewhat angular, glabrous, or initially pubescent but soon glabrescent. Leaf unifoliolate. Petiole 2-8 mm long, glabrous or initially pubescent, petiolule 1-3.5 mm, wrinkled, glabrous or slightly pubescent. Leaflet (stiffly) papery or leathery, ovate or narrowly ovate, rarely elliptic or narrowly elliptic, 3-16.5 × 2-5.5 cm, cuneate to rounded at base, rarely peltate, more or less distinctly acuminate, rarely with a rounded tip; sometimes pubescent when young, but soon glabrous on both sides, midrib strongly impressed above, prominent beneath, with 3-7 lateral nerves on each side, tertiary nerves finely reticulate.

Panicles axillary, single or paired, 1-3(-6.5) cm long, up to 25-flowered, brown-pubescent. Bracts ovate to subulate, 0.5-2 mm long, curved. Pedicels articulate 0.5-1.5 mm below the calyx, densely yellowish brown-pubescent. Flowers heterodistylous, apparently bisexual or sometimes unisexual. Sepals (4-)5(-6), valvate or narrowly imbricate in bud, ovate, 1.5-2.1 × 0.8-1.3 mm, acute or obtuse, more or less flat, brown-pilose outside, glabrous inside. Petals 5, imbricate in bud, oblong or narrowly oblong, 4-8.2 × (0.9)-1.2-2.3 mm, rounded at both ends, pilose outside and pubescent inside, but usually glabrous at base inside, indistinctly 0-3-veined. Stamens united at base for (0.5-)0.8-1 mm, tube glabrous outside, pilose or sometimes glabrous inside; 5 episepalous ones 3-7.2 mm long, filaments pilose in lower half, anthers 0.8-1.5 × 0.5-0.9 mm; 5 epipetalous ones rudimentary, 1.7-3(-3.8) mm long, filaments pilose, anthers lacking. Pistil 1, 1.8-8.2 mm long, ovary ca. 1.5 mm long, yellowish-brown pilose; style pilose; stigma more or less prominent, lobed.

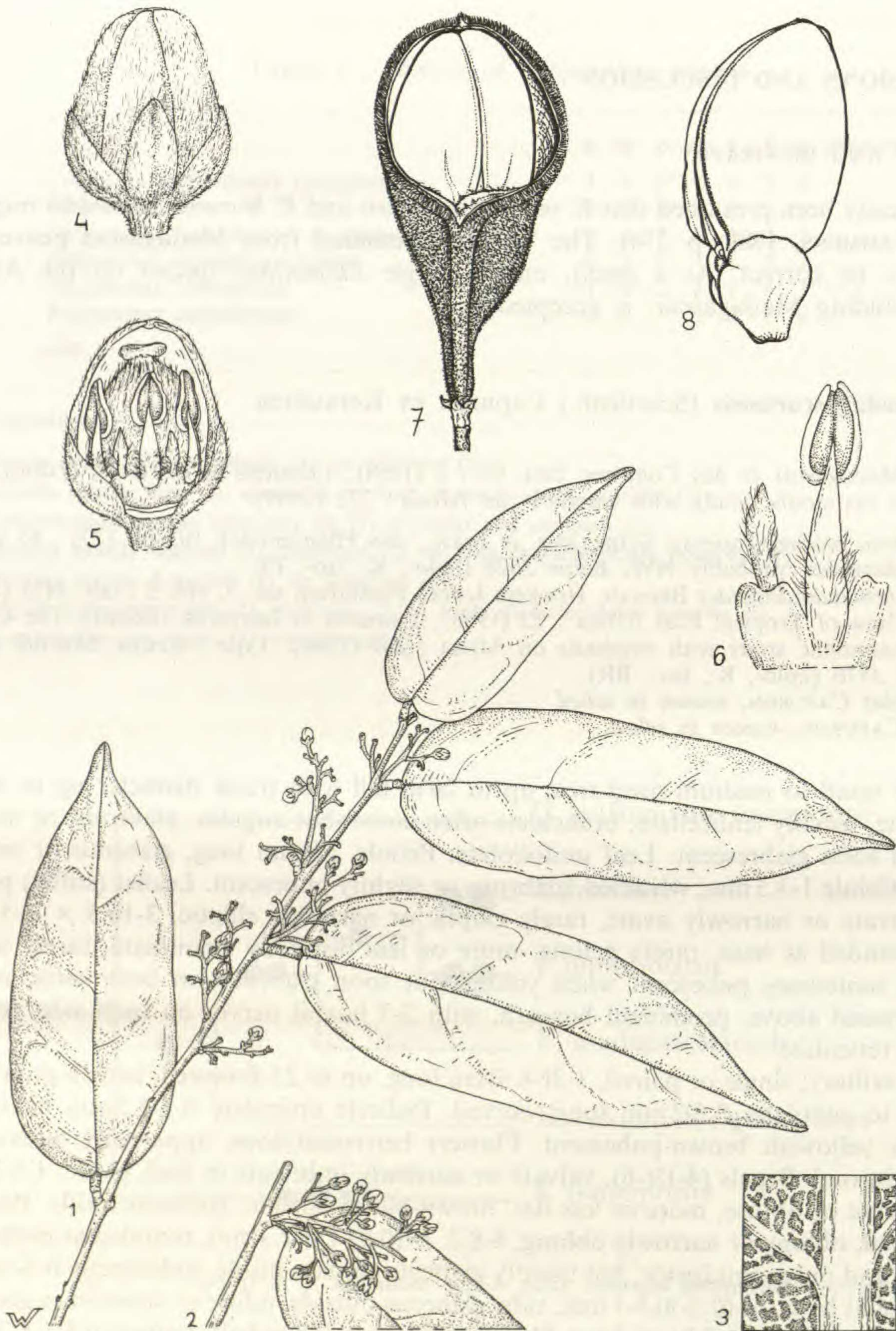


Fig. 2. — *Ellipanthus madagascariensis* : 1, flowering branch $\times 2/3$; 2, inflorescence $\times 2/3$; 3, detail of lower surface of leaflet $\times 6$; 4, flower bud $\times 6$; 5, opened flower bud, showing stamens and pistil $\times 6$; 6, rudimentary and fertile stamen $\times 12$; 7, follicle with protruding seed $\times 2$; 8, seed $\times 2$. (1-6, Baron 5626; 7-8, Reitsma & de Wilde 143).

Follicle oblique-ellipsoid, 2-2.8 × 0.8-1.1 × 0.8-1 cm, stipe up to 8 mm long, not always evident; apex acute or with up to 3 mm long mucro; pericarp somewhat woody, opening lengthwise along the ventral suture, densely golden-yellow or orange-brown tomentose outside, glabrous inside. Seed 1, ovoid or ellipsoid, 11-18 × (5-)8-10 × 5-8 mm, sarcotesta (3-)6-7 mm long, enveloping the basal part of the seed; radicle almost apical but somewhat dorsal; cotyledons thick; endosperm thin or rudimentary.

SPECIMENS EXAMINED. — MADAGASCAR : probably NW, fl., *Baron 5626* (K, P, type); Analamazaotra, fl., *Louvel 46* (P); Ravimaviotra, fl., *Louvel 200* (P); Vatoamala, fl., *Louvel 230* (P); eastern coast, Mananara, fl.b., y.fr., *Perrier de la Bâthie 2098* (P); Ambohitralanana, fl. May, *Réserves Naturelles de Madagascar 9993* (P); Antalaha, Ambohitralanana, fr. July, *Service Forestier de Madagascar 7498* (P); N of peninsula Masoala, Mahalevona valley, fr. Dec., *SF 8741 (Capuron)* (P); SW of Antalaha, Andrakaraka forest, fr. Sept., *SF 9240 (Capuron)* (P); Bekolosy massif, Manongarivo, Sambirano, fl. Sept., *SF 11435 (Capuron)* (P); Diego-Suarez, Ankotekona, fl. May, *SF 15920* (P); Tsarahonenana, N Befandriana distr., between Andrafiabe and Ambato, fr. May, *SF 19067* (P); Analamanara, near Tsaratanana, between Antsirabe-Nord and Sambava, fr. Oct., *SF 24905 (Capuron)* (P); Anosibe, Moramanga distr., Ankazomanitra, y.fr. Nov., *SF 26811* (P); between Tsaratanana and Analamanara,

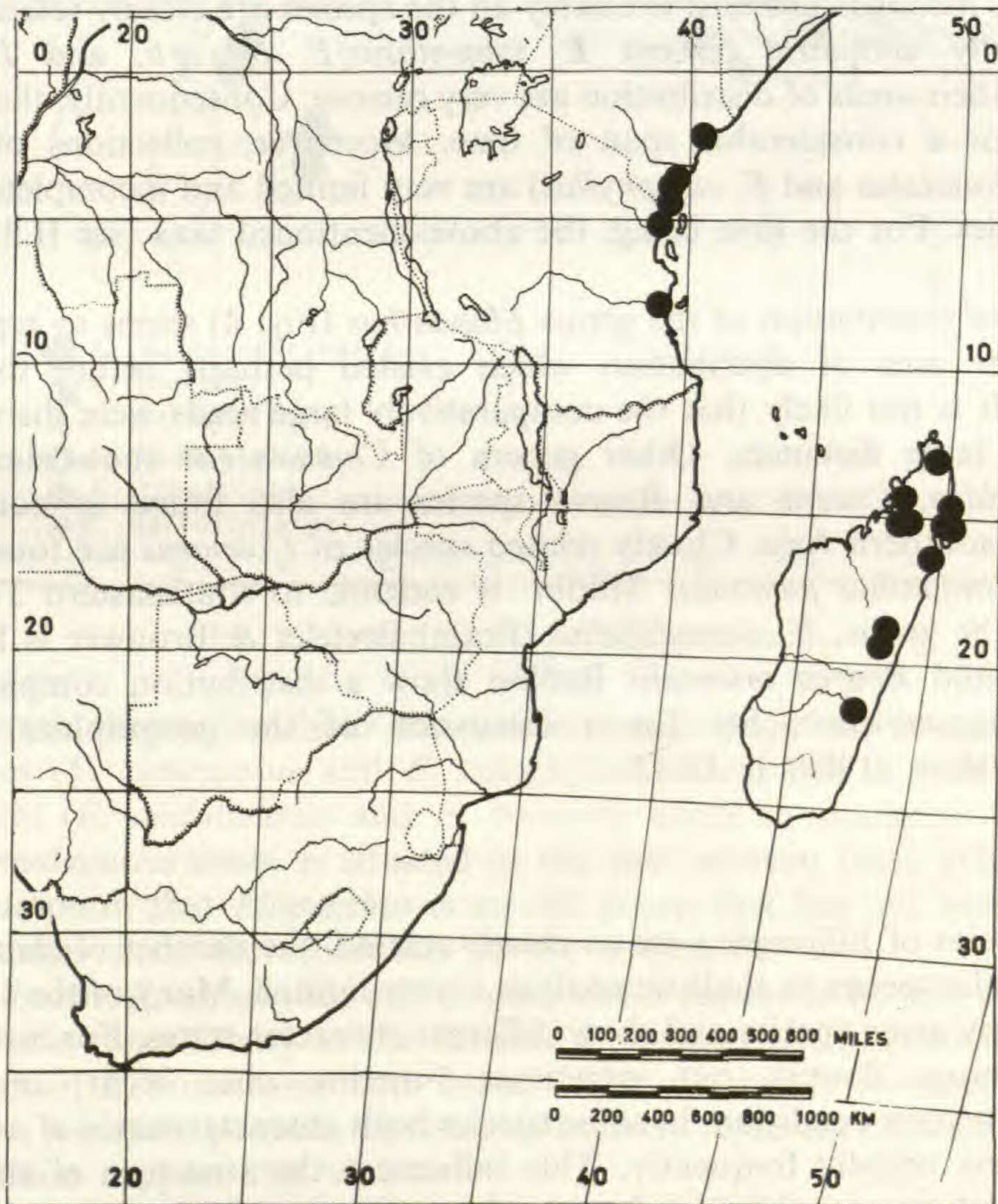


Fig. 3. — Distribution of *Ellipanthus madagascariensis*.

Sambava-Vohémar, Nosiarina-Antisirabe-Nord, y.fr. Mar., *SF 27642 (Capuron)* (P); Sambava-Antalaha, W of Ambodipont-Isahana, near Ambinanifaho, fr. Apr., *SF 27724 (Capuron)* (P); km 45 Moramanga-Anosibe, W of Antanandava, y.fr. Nov., *SF 28405 (Capuron)* (P); W Befandriana, Ankobakobaka, fr., *SF 30030* (P); Andrambovato, E of Fianarantsoa, Fort Carnot, fl. Oct., *SF 256R133* (P). — KENYA : Kilifi Distr., Arabuko-Sokoke F.R., fl. Sept., *Beentje 2314 (WAG)*; Malindi Distr., Mida, fl. Oct., *Dale 3573 (EA, K)*; fr. Apr., *Dale 3876 (BR, K, type)*; Kwale Distr., Buda Mafisini F., 8 miles WSW of Gazi, fr. Aug., *Drummond & Hemsley 3954 (B, BR, K)*; Kwale Distr., Buda F., fr. Mar., *Faden 74/292 (EA, K, WAG)*; Lamu Distr., Witu F., Feb., *Faden 77/570 (BR)*; Kwale Distr., Muhaka F., Mar., *Faden 77/602 (BR, K)*; Kilifi Distr., Gede F., fr. Oct., *Gachathi 200/82 (EA)*; Lamu Distr., Witu F., fr. Nov., *Gathii 125 (EA)*; Malindi Distr., Jan., *Greenway EAH 12580 (EA)*; Lamu Distr., 5 km N of Klitu Ranger F. Post, Feb., *Katende 1750 (EA)*; Kwale Distr., Shimba F., fl.b. Jan., *Katende & Lye 4797 (EA, K)*; Kilifi Distr., Arabuko N.F., fl. Mar., *Padwa B 910 (BR, EA)*; Kilifi Distr., S of Jilore F. Station, fr. Nov., *Perdue & Kibuwa 10056 (BR, EA)*; 9 km E of Bamba, Ganze road, fr. Nov., *Reitsma & J. de Wilde 143 (WAG)*; Kwale Distr., Muhaka F., Feb., *Robertson & Luke 4558 (WAG)*; Gedi, fr. Mar., *Trump 103 (EA, K)*. — TANZANIA : Tanga Distr., Nyamaku, y.fr. July, *Faulkner 2009 (EA, K)*; fr. Dec., *Faulkner 2109 (B, BR, K)*; fr. Jan., *Faulkner 2118 (B, BR, K)*; fl. July, *Faulkner 2158 (B, BR, EA, K, LISC)*; Utete Distr., Ngubuluni F.R., Kibiti, fr. Dec., *Shabani 291 (EA)*.

The Asiatic species of *Ellipanthus* closely resemble each other and they also have a certain resemblance to *E. madagascariensis*. Probably all the species are closely related. However, the species are usually allopatric (except *E. tomentosus/E. beccarii*, and *E. tomentosus/E. calophyllus*), and their areas of distribution are very remote. Consequently, their isolation must have prevailed for a considerable span of time. Moreover, collections of several species (especially *E. unifoliolatus* and *E. calophyllus*) are very limited and incomplete which hampers comparative studies. For the time being, the above-mentioned taxa (see II.3) are maintained on specific level.

The pattern of distribution of the genus *Ellipanthus* (Fig. 4) seems to represent remnants of a much larger area of distribution which existed perhaps before the separation of Gondwanaland. It is not likely that the comparatively large seeds were distributed in recent times over such large distances. Other genera of *Connaraceae* show similar patterns of distribution. *Agelaea*, *Cnestis* and *Rourea* species are also found in continental Africa, Madagascar and southern Asia. Closely related species of *Connarus* are found in Africa and Asia, whereas *Vismianthus punctatus* Mildbr. is endemic to southeastern Tanzania and the other species of the genus, *V. sterculiifolius* (Prain) Breteler & Brouwer is Burmese. *Cnestis polyphylla* Lam, and *Rourea orientalis* Baillon show a distribution comparable to that of *Ellipanthus madagascariensis*. See for a discussion of the geographical distribution of *Connaraceae* LEMMENS (1989) p. 11-13.

2. PHYLOGENY

Since the species of *Ellipanthus* are so closely related, the number of characters useful for the distinction of the species in cladistic analysis is very limited. Many of the characters are not constant within any given species and show different character-states. For instance, *E. beccarii* usually has 4-merous flowers, but sometimes 5-merous ones occur, and *E. tomentosus* demonstrates the reverse condition. In some species both character-states of a certain character occur more or less equally frequently. This influences the structure of the tree : the tree contains 4 "partial apomorphies", where a character-state changes from plesiomorphic to apomorphic for only part of the otu.

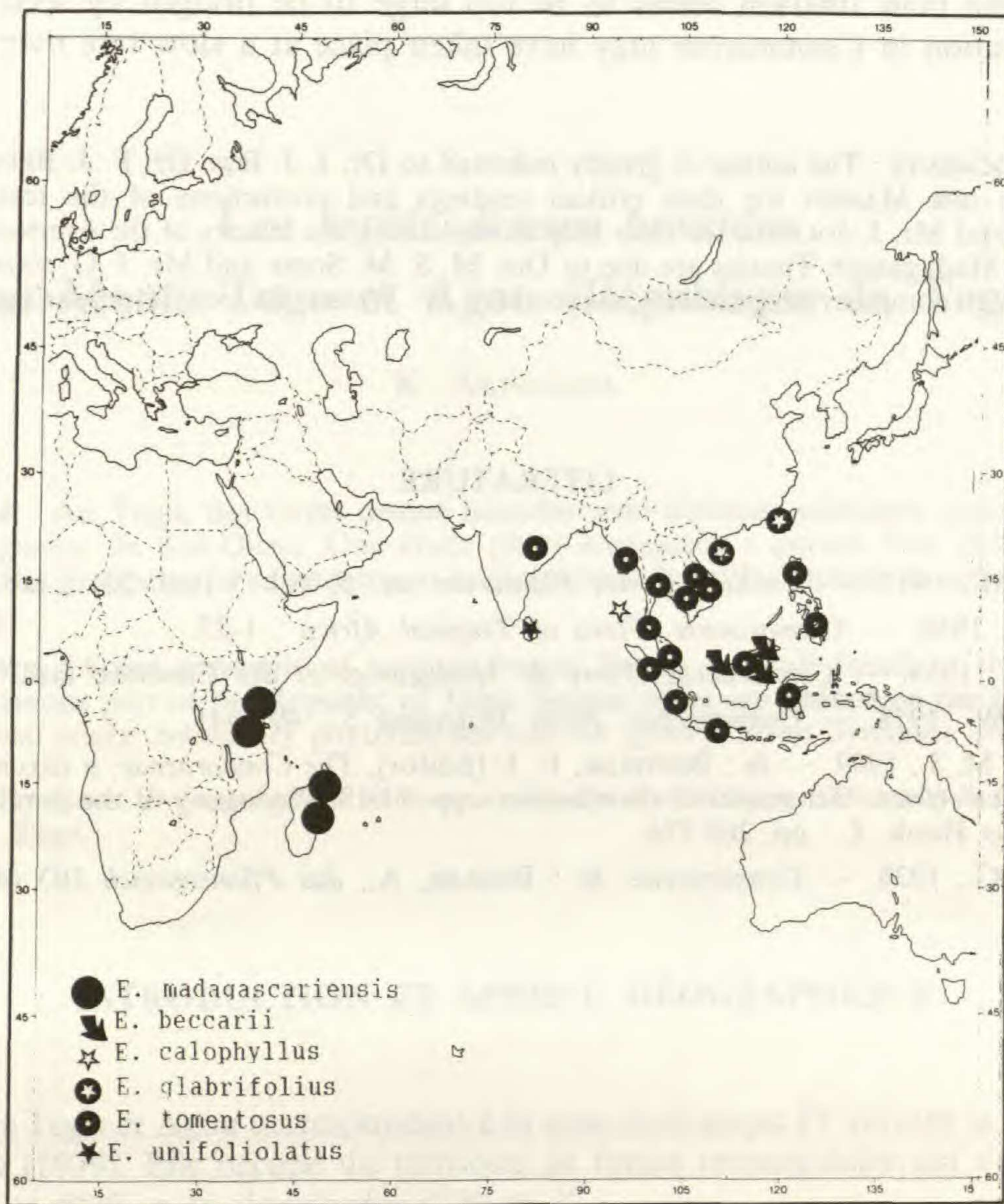


Fig. 4. — Distribution of *Ellipanthus* species.

The cladogram shows that both the species which might be considered as the most “primitive” ones (*E. tomentosus* and *E. calophyllus*/*glabrifolius*) as well as the two most “derived” species (*E. unifoliolatus* and *E. beccarii*) occur in southern Asia. The African species, i.e. *E. madagascariensis*, is situated in the tree between these extremes. This might support the assumption that *Ellipanthus* is an old group that has not been subject to great evolutionary changes since the separation of the continents.

The poorly known *E. calophyllus* and *E. glabrifolius* appear to be very closely related, and they seem to have a close affinity to the variable *E. tomentosus*; in particular, they are very close to specimens of *E. tomentosus* from India, which are usually considered to represent *E. neglectus* Gamble. It is quite possible that they collectively represent only a single species; their areas of distribution support this view.

The populations of *E. madagascariensis* in Madagascar, Kenya and Tanzania might have been separated since the disconnection of Madagascar from the African continent. The

distance of more than 1000 km seems to be too large to be bridged by seed dispersal. As discussed, evolution in *Connaraceae* may have taken place at a slow rate over an extremely long period.

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